Improving and reconstructing data about the network between Orthoptera and flowers in Southeast Asia

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Abstract

Flower visitation by orthopterans, particularly by taxa from Southeast Asia, was only recently brought to light in a report on the diversity and network of 41 orthopteran taxa from Southeast Asia visiting flowers of 35 plant taxa. Continued efforts to document flower visitation by orthopterans have led to 104 new incidences of flower visitation by orthopterans, including 17 new orthopteran taxa. A total of 247 incidences of 58 flower-visiting orthopteran taxa visiting 71 genera of flowers are reported here. In accordance with previous studies, the subfamily Phaneropterinae remains the most prominent flower-visiting orthopterans reported in Southeast Asia and is very likely undisputedly floriphilic. Using a dataset from previous years, the phylogenetic signals of flower-visiting orthopterans and the floral traits of the plant taxa visited are also discussed. However, we recommend caution against drawing too much inference at present owing to the unresolved phylogenetic relationships between the taxa involved and the incompleteness of the current dataset. Therefore, this paper primarily offers an updated list of flower-visiting orthopteran taxa and the flowers they visited. For a more comprehensive understanding of the flower-visiting orthopterans in the region and their ecological impacts, continued natural history research is needed.

Keywords

florivory, insect–plant interaction, natural history, pollination

Introduction

Orthoptera is an order of insects comprised of approximately 30,000 valid extant species of grasshoppers (suborder Caelifera), crickets, and katydids (suborder Ensifera) (Cigliano et al. 2024). Orthopterans are not typically considered frequent flower visitors or pollinators (Wardhaugh 2015). Consequently, in many studies on flower-visiting arthropods, data on orthopterans are neglected and excluded from analyses because they are rarely encountered or are not considered effective pollinators (Goodwin et al. 2021. Chapman et al. 2023. Stark et al. 2023). However, throughout the world, orthopterans have been sporadically reported to visit flowers (e.g., Gangwere 1961, Ingrisch and Köhler 1998, Gwynne 2001, Micheneau et al. 2010, Pedersen et al. 2018, Torres-Cruz et al. 2024). Pedersen et al. (2018) and Suetsugu and Tanaka (2014) further postulated that regular flower visitation among orthopterans may be an important precursor for orthopteran–plant mutualism through pollination services. This suggests the importance of documenting previously unknown flower-visiting orthopterans that may already be offering beneficial services to plants.

The diversity of flower-visiting orthopterans from Southeast Asia was recently brought to light in a pivotal paper by Tan et al. (2017a) in which a total of 41 orthopteran species from Southeast

Asia were reported to visit flowers belonging to 35 plant species, confuting earlier reports that orthopterans are rare flower visitors (e.g., Wardhaugh 2015). Instead, it is likely that these insects are simply overlooked (Tan et al. 2017a). Tan and Tan (2018a) also revealed evidence of a flower-visiting katydid helping with pollination. Occasionally, orthopterans found in Southeast Asia have been reported to regularly frequent flowers (Suetsugu and Tanaka 2014, Ghosh and Pal 2017) as much as or more frequently than other known flower-visiting insects such as the Hymenoptera (Sanfiorenzo et al. 2018, Tan et al. 2019, Huang et al. 2021).

Tan et al. (2017a) postulated that their findings are likely to be a gross underestimation of the number of flower-visiting orthopterans in Southeast Asia, especially since it is often difficult to observe relatively rare synchronous flowering events typical of Southeast Asian forests. Considering that many orthopterans from the region were only recently discovered (Cigliano et al. 2024) and that little is known about them beyond their original descriptions, flower visitation by many more orthopterans may also be undocumented.

Indeed, since Tan et al. (2017a), more flower-visiting orthopterans were observed between 2017 and 2024 throughout Southeast Asia, including the Philippines, Vietnam, and new records from Peninsular Malaysia and Brunei Darussalam. Observations of orthopterans in the understory plants during synchronous flowering events were also made. This warrants a more comprehensive and up-to-date study of the bipartite network (or affiliation network) between orthopterans and the corresponding flowers they visit to better illustrate the diversity of flower-visiting orthopterans from the region. Also, unlike in Tan et al. (2017a), the bipartite network should be arranged according to the phylogeny of Orthoptera to offer a visualization of the diversity and frequency of flower visitation by different clades of orthopterans. Here, we present this bipartite network and examine the form (e.g., solitary, inflorescence), color, symmetry (radial or bilateral), and position of the flowers (at the terminal or axillary buds) of the visited floral taxa.

Materials and methods

Photographic records were obtained between late 2017 and middle 2024 in Singapore, the Philippines (including Luzon Island, Siargao Island, and Mindanao Island), Sabah in Borneo, Belait in Brunei Darussalam, Bach Ma National Park in Vietnam, and Johor State in Peninsular Malaysia. Both adults and nymphs observed to visit flowers were photographed as evidence of both the visitor and the visited flowers, especially important in the event when either or both the orthopterans and flowers could not be collected. All data are available as Suppl. material 1. The criteria used to consider an orthopteran as a flower visitor follow those in Tan et al. (2017a). Species identification of the orthopterans, whenever possible, was performed by MKT. Otherwise, the lowest possible taxonomic rank was used, primarily for nymphs. Plants were identified to genus level whenever possible; it was not always possible to verify plant species' names based only on images.

To visualize and summarize the updated network of orthopteran taxa and visited flower taxa, an interaction network was constructed using the 'plotweb' function in the bipartite package (Dormann et al. 2008) in R software v.3.3.3 (R Core Team 2016). Instead of using the default method "cca" to minimize the number of crossings between the orthopteran and plant levels, the orthopteran taxa were arranged according to their relative placements in the most recent orthopteran phylogenies by Mugleston et al. (2013, 2018), Chintauan-Marquier et al. (2016), and Song et al. (2015, 2018). The plant taxa were arranged according to the alphabetical order of their family names.

For graphical analysis, the floral traits of the plant taxa visited by orthopterans, including the form (e.g., solitary, inflorescence), color, symmetry (radial or bilateral), and position of flowers (at the terminal or axillary buds), were determined for each plant taxon. The floral traits were obtained from the National Parks Board Singapore Flora and Fauna Web database (www.nparks.gov.sg/florafaunaweb). Bar plots were used for the visualization of the traits of the florals visited by orthopterans.

Results

In total, 247 incidences of 58 flower-visiting orthopteran taxa visiting 71 genera of flowers are reported here (Fig. 1). In total, 107 new incidences of flower visitation by orthopterans and 17 new orthopteran taxa were added to the ones by Tan et al. (2017a). Forty-five taxa of ensiferans (78% of all orthopteran taxa) were observed to visit flowers, which is more than the 13 taxa of caeliferans (22% of all orthopteran taxa). Eighteen genera of flowers were visited by both ensiferans and caeliferans. Thirty-six genera of flowers were visited exclusively by ensiferans, and 17 genera of flowers were visited exclusively by caeliferans.

Among the ensiferans, the most prominent flower visitors were those from the subfamily Phaneropterinae (21 taxa), accounting for 36% of all taxa and 45% of all records on flower visitation (i.e., 110 incidences). *Phaneroptera* Serville, 1831, *Conocephalus* Thunberg, 1815, and *Nisitrus* Saussure, 1878 were the top three genera observed to visit the most diverse genera of flowers (Fig. 1). *Phaneroptera* visited flowers from 20 genera from 7 families, *Nisitrus* visited 15 genera from 10 families, and *Conocephalus* visited 12 genera from 6 families.

Among the caeliferans, only taxa from the subfamilies Pyrgomorphinae (family Pyrgormorphidae), Acridinae, Oxyinae, Catantopinae, and Cyrtacanthacridinae (family Acrididae) were observed to visit flowers (Fig. 1). The genera *Xenocatantops* Dirsh, 1953 and *Valanga* Uvarov, 1923 were recorded to visit the greatest number of genera of flowers at 19 genera and 15 families and 8 genera and five subfamilies, respectively.

The orthopterans were observed to most often visit genera of flowers from the family Asteraceae, totaling 16 genera. Some genera of flowers, such as *Ageratum* L. 1753 not Mill. 1754, *Bidens* L., *Prexalis* Cass., and *Sphagneticola* O. Hoffm., were observed to be visited by most species of orthopterans, with 10, 7, 15, and 10 taxa, respectively (Fig. 1). Following Asteraceae, orthopterans were observed to visit 11 genera of flowers from the family Fabaceae, although most genera in this family were visited by one or two orthopteran taxa each. Other notable genera visited by orthopterans include *Costus* L. (visited by seven orthopteran taxa), *Dillenia* L. (six), *Claoxylon* A. Juss (five), and *Lantana* L. (seven).

Flowers observed to be visited by the greatest number of orthopteran taxa occurred in clusters/inflorescence (23 genera of flowers, 32.4%), were head/capitulum (11, 15.5%), or were solitary/simple (10, 14.1%) (Fig. 2A); they were either white (18, 25.4%), yellow (15, 21.1%), or pink and purple in color (7 each, 10.0%) (Fig. 2B). Flowers that are radially symmetrical (52, 73.2%) instead of bilaterally symmetrical (15, 21.1%) (Fig. 2C) or located terminally (40, 56.3%) rather than from axillary buds (22, 31.0%) (Fig. 2D) were observed to be visited by more orthopterans.

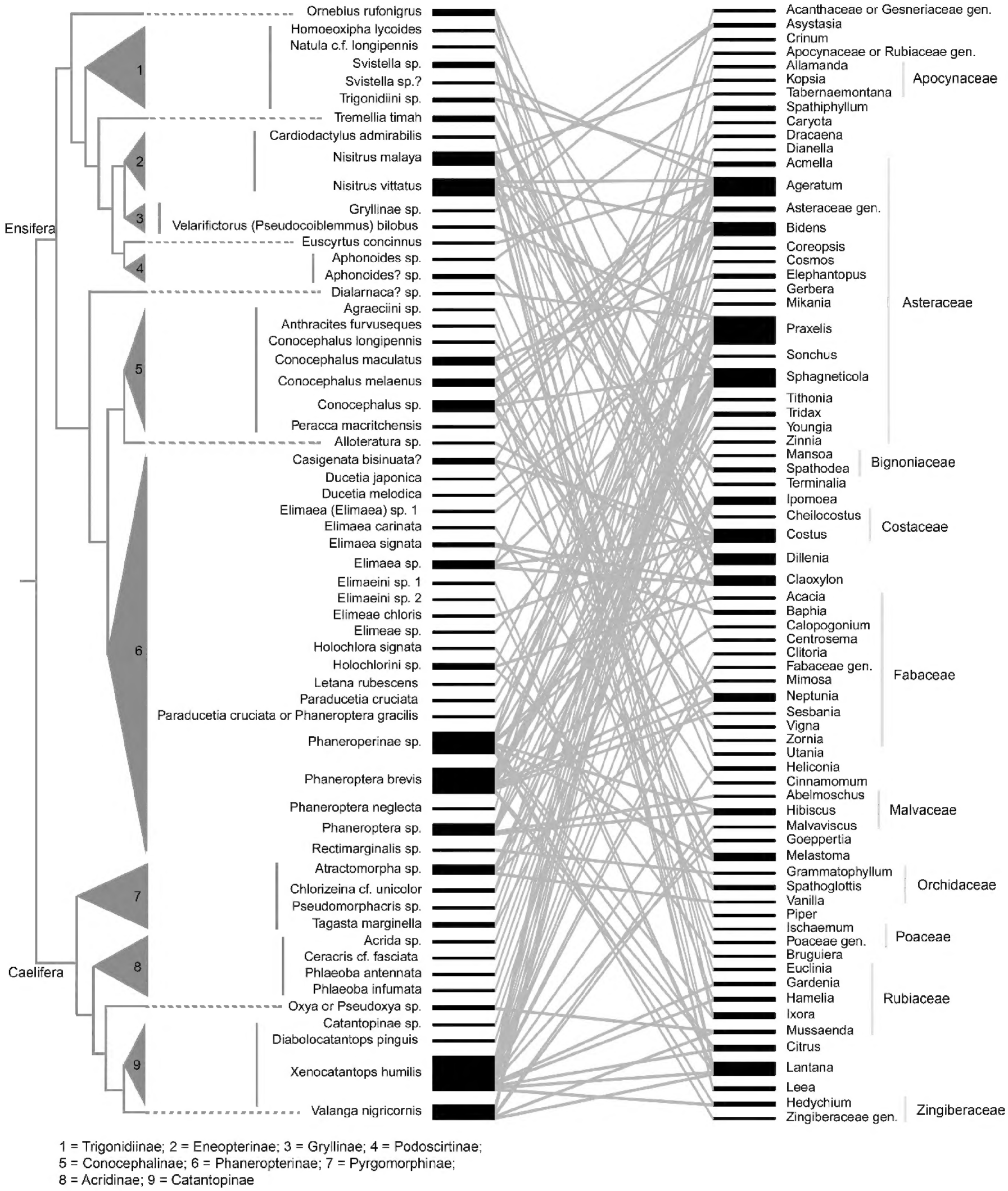

Fig. 1. The interaction web between 58 flower-visiting orthopterans (right column) and 71 genera of flowers (left column) in Southeast Asia based on 247 observations. The orthopterans on the right are arranged according to orthopteran phylogeny, and the flower genera are arranged alphabetically after arranging according to family names in alphabetical order. The dendrogram illustrating the relationships between the orthopteran groups is based on phylogenies by Mugleston et al. (2013, 2018), Chintauan-Marquier et al. (2015), and Song et al. (2015, 2018).

Discussion

Flower visitations by 17 orthopteran taxa were documented for the first time as sampling effort and sites increased. Specifically, new incidences of flower visitation by orthopterans and new orthopteran taxa represented 43% and 29%, respectively, of all records consisting of new data and published data from Tan et al. (2017a). These include more incidences and taxa of katydids from the subfamily Phaneropterinae visiting flowers—the most prominent flower-visiting orthopterans reported in Southeast Asia. Multiple Phaneropterinae taxa can be found to visit flowers in various habitats, ranging from more open grasslands/shrublands to different forest types. Some noteworthy observations include a species of *Rectimarginalis* Liu & Kang, 2007 visiting a *Grammatophyllum* Blume orchid

in Sabah (Fig. 3A), the forest-restricted species *Casigenata bisinuata* Karny, 1926 in Singapore visiting the panicles of *Cinnamomum iners* Reinw. ex Blume (Fig. 3B), clusters/inflorescences of *Caryota mitis* Lour. (Fig. 3C), the cymes of *Cinnamomum iners* (Fig. 3C), and the petals of *Costus* sp. (Fig. 3D). These observations indicate that this subfamily is a generalist flower visitor, although at the specific level, as some species are more specialists. For example, a mangrove-associated species, *Holochlora signata* Brunner von Wattenwyl, 1891, was observed to visit the flowers of a mangrove tree, *Bruguiera cylindrica* (L.) Bl.. It should further be added that Phaneropterinae can occur in high abundance and diversity in the forest canopy and are often only encountered in such abundance and diversity at light traps (e.g., Tan and Wahab 2018; Tan et al. 2024). Thus, it is not surprising that many of these katydids visit and feed on flowers in the canopy layer of forests, which makes this activity particularly difficult to observe and document. Advances in non-invasive sampling methods in canopies, such as macro-camera traps, may address this in the future, particularly during rare mass flowering events in dipterocarp forests.

That orthopterans from the genera *Phaneroptera* (Fig. 4A, B), *Nisitrus* (Fig. 4C, D), and *Conocephalus* (Fig. 4E), as well as *Xenocatantops* (Fig. 4F, G) and *Valanga* (Fig. 4H), were most frequently observed to visit flowers can be attributed to the fact that they are common and abundant species in places where observations were more readily made. Although Tan et al. (2017a) reported similar results, more visited flower genera are reported here. For example, *Phaneroptera brevis* Serville, 1838 were observed to visit 16 flower taxa compared to 13 taxa in Tan et al. (2017a), and *Xenocatantops humilis* (Serville, 1838) were observed to visit 19 taxa compared to 5. These increases are likely the result of greater observation efforts in the forest and on a broader geographical scale. Interestingly, *Xenocantatops*, typically considered an opportunistic polyphagous, was found to visit more diverse genera and subfamilies of flowers than any of the *Phaneroptera*. This observation corroborates a finding by Tan and Tan (2019b) that *Xenocatantops*, and possibly other polyphagous herbivorous insects, may feed preferentially on floral parts when available.

Other prominent orthopteran groups that were observed to visit flowers include crickets from the families Trigonidiidae (mostly from the subfamily Trigonidiinae) and Mogoplistidae. These small crickets are opportunistic in their feeding preferences, feeding on both plant and animal remains. They also tend to dwell among the leaves and branches of herbs, shrubs, and understory trees where flowers are most accessible. It was not surprising to find that more crickets from Trigonidiidae and Mogoplistidae visit and feed on flowers. On the other hand, the finding of no record of flower-visiting Gryllacrididae in our dataset was unexpected. Gryllacrididae were the first orthopterans shown to pollinate flowers (Micheneau et al. 2010; Krenn et al. 2016). Even during synchronous flowering events in the forest understory where gryllacrids tend to inhabit, no observation of flower visitation was observed. Additionally, predominantly herbivorous katydids from the subfamilies Pseudophyllinae and Mecopodinae, which are also close relatives of Phaneropterinae, do not appear to visit flowers.

Flowers of the families Asteraceae and Fabaceae were most visited by orthopterans. Most of the visited Asteraceae produce heads/capitula, whereas visited Fabaceae produce a diverse range of flower forms, including solitary flowers, racemes, and clusters. Furthermore, most of the visited Asteraceae flowers exhibit radial symmetry, and most of the visited Fabaceae flowers exhibit bilateral symmetry. This suggests that floral traits themselves do not necessarily explain why Asteraceae and Fabaceae are most visited by orthopterans. Instead, it may also be attributed to the free-flowering nature of many of these taxa and their tendency to dominate their habitats. For example, *Bidens*, *Prexalis*, *Neptunia* Lour., and *Mimosa* L. can easily dominate ground vegetation and are highly invasive in some parts of the world, including Southeast Asia (e.g., Lowe et al. 2000; Pandit et al. 2006; Kato-Noguchi 2023; Kato-Noguchi and Kurniadie 2024). Tan et al. (2019) demonstrated that more *Phaneroptera* individuals were observed to visit patches of vegetation with higher abundances of these flowers. Coincidentally, many of the flower genera are also attractive to butterflies,

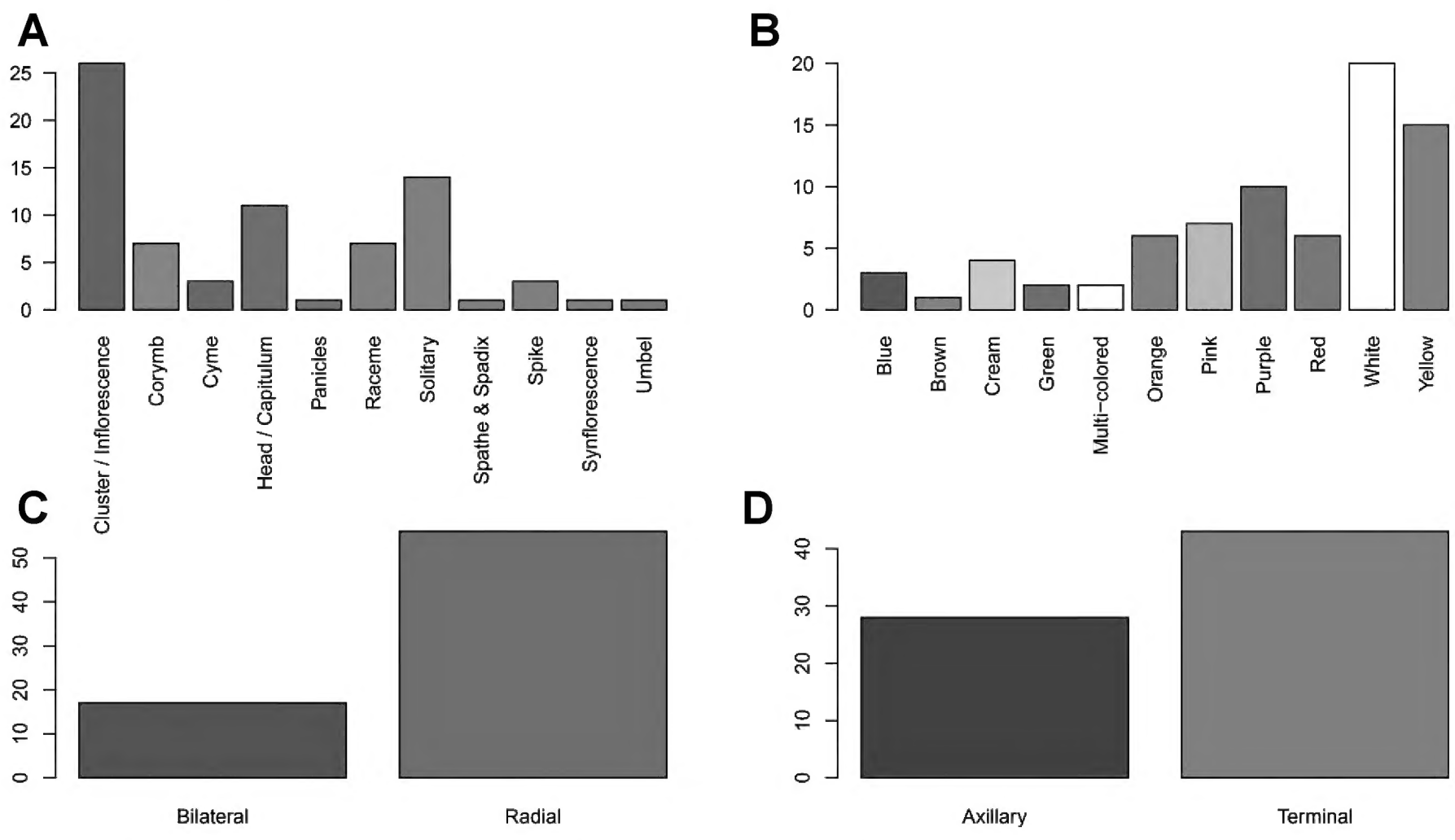

Fig. 2. Bar graphs showing the relative proportions of the **A.** Form; **B.** Color; **C.** Symmetry, and **D.** Position of the flower taxa (not genera) observed to have been visited by orthopteran taxa.

and some taxa have been deliberately planted to attract butterflies in managed parks and gardens. These flower taxa include *Bidens*, *Sphagneticola*, *Melastoma* Blume, and *Lantana* (Soh and Ngiam 2013; Radhakrishnan et al. 2019; Tan et al. 2019). leading to increased encounters with flower-visiting orthopterans.

In general, flower-visiting orthopterans were observed to prominently visit radially symmetrical flowers. It has been hypothesized that bilaterally symmetrical flowers evolved from ancestral radially symmetrical flowers coinciding with the diversification of specialized insect pollinators, thereby suggesting some form of pollinator-mediated selection (Citerne et al. 2010). Perhaps we can also infer that flower-visiting orthopterans are typically opportunistic and generalist florivores or pollinators. *Phaneroptera*, however, exhibit a specific preference for flowers over leaves, as shown by a series of experimental studies (Tan and Tan 2017, 2018a, 2018b, 2019a; Tan et al. 2017b, 2018a, 2018b, 2019; Goh et al. 2019), and are generalist florivores. Other reported prominent flower-visiting orthopterans, including species of *Conocephalus*, feed on a wide variety of plant and animal parts (Willemse 2001). Likewise, *Xenocantatops* and *Valanga* are known to be aggressive pests to a variety of plants (Willemse 2001).

Flower-visiting orthopterans also appear to exhibit a preference for white and yellow flowers. This is congruent with findings by Pickering and Stock (2003) that demonstrated that insects, particularly generalist flower-visiting dipterans, visit preferentially

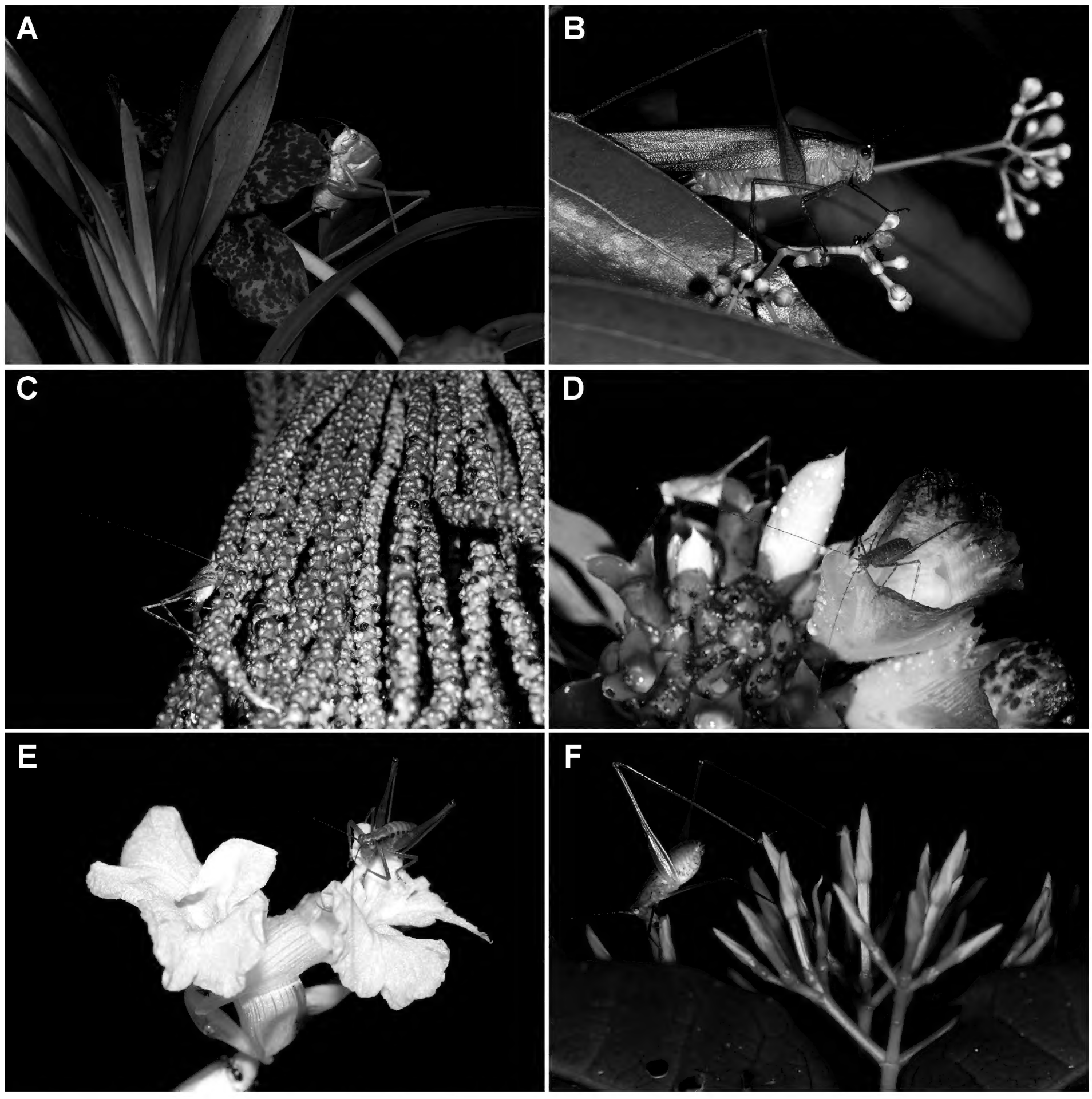

Fig. 3. Flower-visiting Phaneropterinae. **A.** *Rectimarginalis* feeding on a petal of *Grammatophyllum* in Sabah; **B.** *Casigenata bisinuata* on the panicles of *Cinnamomum iners,* and **C.** a cluster/ inflorescence of *Caryota mitis* in Singapore; **D.** Unidentified Phaneropterinae nymphs feeding on the petals and sepals of *Costus lucanusianus* in Singapore, and **E.** Visiting the flower of an unknown Zingiberaceae in the Philippines and **F.** An unknown Apocynaceae or Rubiaceae in Singapore.

white and yellow flowers and colored traps. Likewise, in a series of behavioral experiments, grasshoppers were found to approach yellow targets more frequently than other colors (Bailey and Harris 1991). The ecological significance of this color preference among orthopterans remains unclear. In contrast, only slightly more plant taxa with terminal flowers are frequent by flower-visiting orthopterans compared to those with axillary flowers. The location of the flowers may inform the flower visitor's accessibility to resources and risk of exposure to predation. However, these considerations are also dependent on other floral traits such as size, color patterns and wavelengths outside of human's visible spectrum, and plant height.

Even though the observations presented here offer insights into the traits exhibited by visited flowers, it would be irresponsible to conclude that flower-visiting orthopterans have specific preferences for certain floral traits. A combination of floral traits, as well as the

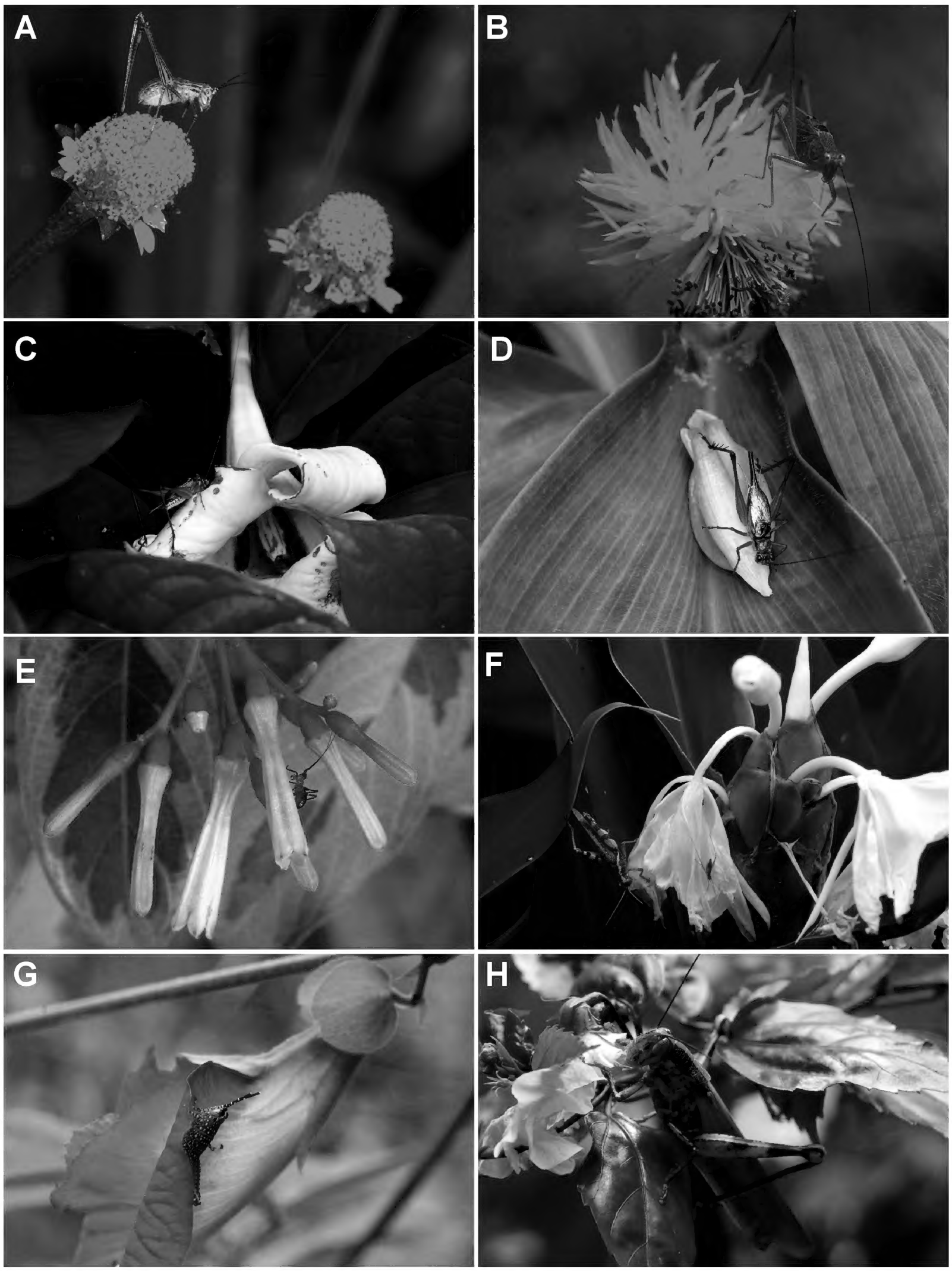

Fig. 4. Frequent flower-visiting orthopterans: **A.** *Phaneroptera* species visiting the head/ capitulum of *Acmella* in the Philippines and **B.** Spike of *Neptunia* in Singapore; **C.** *Nisitrus malaya* visiting the flower of *Euclinia* and **D.** Feeding on the petal of *Costus* in Singapore; **E.** *Conocephalus melaenus* nymph on the cyme of *Hamelia* in Singapore; **F.** *Xenocatantops humilis* feeding on the petals of *Hedychium coronarium* and **G.** *Clitoria ternatea* in Singapore; **H.** *Valanga nigricornis* feeding on the petals of *Hibiscus* in Singapore.

availability (in terms of richness and abundance) of the flowers, play a role in determining how frequently these flowers are visited by orthopterans. There are also other floral traits that may be more useful in understanding the preference for chewing florivores, such as the palatability of flowers (McCall and Irwin 2006), but these are not easily studied, and the few studies that exist are limited to a small number of flower species and florivore subjects (Tan and Tan 2018b).

Beyond flower visitation, questions on whether these orthopterans help with pollination or cause more florivory damage to the plants should also be addressed in further work. Typically, however, florivory is considered less costly for plant fitness than leaf herbivory or seed damage, even though the differences can be subtle. In contrast to leaf herbivory, florivory may increase resource availability per surviving flower. Fertilized ovules in seeds are also considered more valuable than unfertilized ones in flowers (McCall and Irwin 2006). The effectiveness and importance of orthopterans as pollinators are still insufficiently quantified. Future studies combining cost-benefit analysis of both pollination and florivory by orthopterans are crucial to better understand the ecological roles of flower-visiting orthopterans.

In conclusion, this paper offers new incidences of flower-visiting orthopterans to further corroborate previous observations that Orthoptera are more frequent flower visitors than expected. However, with many species from Southeast Asia still undescribed and with unknown natural history, as well as with a vast part of the region remaining unexplored and understudied, we are still extremely far from understanding the actual diversity of flower-visiting orthopterans.

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Supplementary material 1

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Data type: csv

Explanation note: Occurrences of Orthoptera-flower interactions (identified to species and genera), including higher taxon ranks and floral traits.

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